Foraging by Rattus norvegicus on a Radial Maze:
A Test of the Optimal Foraging Model

Shelley May

Algoma University College

1991 - 1992

Running Head: FORAGING ON A RADIAL MAZE

Abstract

To determine which model (Familiarity, Escape Routes, or Food Danger) best predicts where a rat will move food items varying in weight, eight male Long-Evans hooded rats (Rattus norvegicus) were allowed to forage on a four-arm radial maze. In Condition 1, food items varying in weight were placed on the arms of the maze; in Condition 2, food items varying in weight were placed in the center of the maze. In Condition 1, the rats increasingly carried food to the center of the maze as the food size increased. Results were confirmed by statistical analyses $F(5,35)=20.40$. In Condition 2, the rats increasingly carried food to the arms of the maze as the food size increased. Results were confirmed by statistical analyses $F(5,35)=4.00$. This study provides support for the food danger model as well as new information concerning the factors that influence optimal foraging in rats. The implications and limitations of foraging on the maze are discussed.

OPTIMAL FORAGING THEORY

One reason there has been an increased interest in foraging behavior is the emergence of a theoretical perspective known as optimal foraging theory (OFT). This perspective is one application of the idea that individuals act in such a way as to maximize their inclusive fitness. Optimal foraging theory answers the question "What should animals do?" (Mellgren, Misasi, and Brown, 1984).

Optimal foraging theory assumes that the fitness associated with an animal's foraging behavior has been maximized by natural selection, subject to certain constraints. The basic argument is as follows: Behavior in general, and foraging behavior in particular, show heritable variation; this entails variation in the contribution to subsequent generations. There is a range of possible foraging behaviors. In other words, there are constraints in the system. For example, an animal may or may not be able to alter its rate of encounter with a particular food type by altering its own behavior. Finally, natural selection will favor those individuals in a population which contribute the most to subsequent generations. Hence, natural selection will result in a change with time of the average foraging behavior in the populations, towards that foraging behavior in the range of possible behaviors which gives maximum fitness (Pyke, Pulliam, and Charnov, 1977).

Optimal foragers should select ways to collect food that are highly efficient or maximize the energy accumulated for the time and effort expended. Although rate of energy accumulation may be a primary concern for some foragers, defensive concerns as well are of importance for other animals. Many animals are constantly susceptible to predation or food thievery while foraging. One adaption to this problem in a number of species is central place foraging. Central place foragers often carry food from the patch (defined as a discrete location in space where food is found) to a central protected area or home base (defined as the place where the animal brings the food) before consuming it or feeding it to offspring. Carrying food to safety to consume reduces the time an animal exposes itself and its food to predation or thievery (Roberts, Phelps, and Schacter, 1989). There remains however, a question of what defines "safety".

In a recent series of articles, Lima and his colleagues have argued that many animals adopt an optimal trade-off between the demand for foraging efficiency and the demand for minimal exposure to predation (Lima, 1985; Lima and Valone, 1986; Lima, Valone, and Caraco, 1985). Their model holds that animals tend to eat small food items where they are found in the patch, because these items are consumed rapidly and involve little handling time during which the animal is exposed to predation. Large food items require long handling times and therefore should be carried to safety for consumption.

Lima, et al. (1985) placed food items of varying sizes at various distances from the safety of trees and observed how grey squirrels (_Sciurus carolinensis_) foraged. Squirrels ate small food items where they found them, but carried large food items back to the safety of a tree before consuming them.

Some observational data of wild rats suggests that these rodents also engage in central place foraging. Norway rats (_Rattus norvegicus_) and roof rats (_Rattus rattus_) construct underground burrows consisting of interconnecting tunnels and chambers (Flannely, Kemble, and Hori, 1986; Flannelly and Lore, 1977; Lore and Flannelly, 1978; Pisano and Storer, 1948). Wild rats have been observed to carry large pieces of food to their burrows or to a protected spot near the burrow. In some cases, rats have been seen to engage in larder hoarding (defined as the concentration of all food at one site), or storing food in a safe place for later consumption (Barnett, 1975; Covich, 1987; Flannelly and Lore, 1977). Therefore, it has been suggested that rats would appear to be excellent subjects for the study of central place foraging.

STUDIES IN THE RADIAL MAZE

Although the radial maze traditionally has been used as a tool for studying animal memory (Olton and

Samuelson, 1976; Roberts, 1984), some recent investigations suggest that it may also be used to examine foraging. A radial maze has a circular center platform, and four arms radiating from the center. Phelps and Roberts (1989) argued that if the arms of a radial maze are analogous to food patches and the center of the maze functions as a home burrow or place of safety, then this apparatus may elicit in laboratory rats some of the central place foraging behaviors found in wild rodents.

In a series of experiments, Phelps and Roberts (1989) systematically explored the variables that suggest that rats treat the center of the maze as a central place of safety, and that they tend to carry large food items from the arms of the maze to the center for consumption.

Food items consisting of pieces of cheese varying in weight (0.05 - 5.40 g) were placed on the ends of the arms of a four-arm radial maze. Rats allowed to forage ate small food items on the arms, but increasingly tended to carry items to the center of the maze for consumption as item size increased (Phelps and Roberts, 1989). These findings agree well with predictions from the foraging efficiency predation risk trade-off model advanced by Lima et al. (1985) and Lima and Valone (1986).

Ilersich, Mazmanian, and Roberts (1988) used a four-arm radial maze to study foraging in rats. Each arm of the maze was defined as a patch and contained four feeding stations. Each patch contained a total of 20 45-mg food pellets, with the first feeding station in each patch baited with 1 pellet and the remaining stations baited with 1, 5, or 13 pellets. In Experiment 1, one group of rats was tested with feeders open and food readily accessible, and in Experiment 2, another group was tested with metal covers on the feeders, which necessitated extra time to gain access to food. With open feeders, the rats visited each feeder in a patch in the order in which they encountered the feeders, from the center of the maze to the end of the arm. The rats in the group with the covered feeders often visited the feeders containing 5 or 13 pellets first and the feeders containing 1 pellet last (see Figure 1). In Experiment 2, it was found that the rats switched readily between these two foraging strategies when tested with covered and open feeders on alternate sessions. The extra time and effort required to uncover food appeared to produce selective foraging in rats.

Insert Figure 1 about here

The interesting observation made in the experiments was that the rats foraged selectively when the food was covered, but not when the feeders were open. The observation that the rats visited the covered feeders containing the largest quantities of food first would seem to be a good example of optimal foraging. Since time and energy were expended in uncovering food, the rate of food consumption was maximized by visiting the most valued feeders first. When the feeders were open, the rats simply visited feeding stations in order, from Station 1 to Station 4 in each patch Thus, as a result, the pattern of the maze may be important as an analogue of the natural habitat within which wild rats live and forage (Ilersich, Mazmanian, and Roberts, 1988).

Whishaw and Tomie (1989) conducted an experiment to examine the influence that the size of food pellets has on hoarding behavior. Hoarding has been operationally defined as the handling of food to conserve it for future use (Vander Wall, 1990). Rats were allowed to forage for different sized (20- to 500-mg) food pellets from a cage attached to a straight alley or from a cage placed in the center of an 8-arm radial maze.

Figures 2 and 3 show the frequency of times in which a rat sits and eats a piece of food (sits), takes the piece of food in his mouth and eats it (eat), or takes the piece of food and stores it for later (hoard). Small food pellets were swallowed at the food source. Medium-sized food pellets were grasped by mouth, and, after the rat stepped away from (dodged) the food source, they were eaten as the rat adopted a sitting posture. Large food pellets were hoarded to the adjacent enclosure (Whishaw and Tomie, 1989). It is presumably more adaptive, in terms of energy conservation and risk, to hoard larger pieces of food rather than smaller pieces, as might be suggested by optimal foraging theory (Pyke, Pulliam, and Charnov, 1977).

Insert Figure 2 about here

Insert Figure 3 about here

Roberts (1989) conducted several experiments that suggested how rats show central place foraging on the radial maze under certain conditions. The apparatus used was a six-arm radial maze. The major independent variable studied in the experiment was the amount of food placed at the end of each arm of the maze. The quantity of food was varied by placing single pieces of food (cheddar cheese) varying in weight (0.05, 0.45, 0.90, 1.80, and 2.70 grams) on the ends of each arm of the maze. On each testing session, one cube of each size was placed on the end of each of five arms of the maze. The sixth arm contained no food. Thirty-six male hooded rats were allowed to forage for these food items once a day for 18 days. An exact record of each rat's foraging behavior was kept.

The results are shown in Figure 4; one curve plots the proportion of opportunities on which items of different size were eaten where they were found on the end of an arm, and the other curve plots the proportion of opportunities on which items were carried to the central platform of the maze for consumption. Items weighing only 0.05 grams almost always were eaten on the arm, whereas large items weighing 1.80 grams and 2.70 grams almost always were carried to the center of the maze. At the intermediate quantities of 0.45 grams and 0.90 grams, rats both carried to the center and ate on the arm of the maze (Roberts, 1989).

Insert Figure 4 about here

These data suggest two important things. First, rats appear to treat the center of the radial maze as a place where food items may be consumed in safety. They treat the arms of the maze as a place where predation or food thievery is possible. Second, food carrying decisions are strongly controlled by item size, and the tendency to increase carrying with increases in item size agrees with Lima's model of central place foraging (Roberts, 1989).

The Size Hypothesis

Several hypotheses have been offered to explain the strong attraction of the center of the radial maze for food-carrying rats. One possibility is that rats prefer to eat on the central platform provided by the center simply because it provides a large area. The central platform used was 35 cm in diameter, whereas the arms were only 9 cm wide. If rats fear falling off the maze, the wide central platform provides greater safety because animals can eat at a safe distance from the edge of the platform. One alternative hypothesis is that rats are attracted to the center of the maze because all of the arms intersect at that point. The suggestion that rats may perceive the center as that area of the maze with the maximum number of escape routes leads to the prediction that animals should carry food to the center regardless of its size (Roberts, Phelps, and Schacter, 1989).

As a test of the above hypotheses, an experiment was carried out using the mazes depicted in Figure 5. All of these mazes contained open arms and centers but varied in the locations at which wide circular platforms were placed. Maze A was the standard radial maze, with a 35 cm wide circular central platform and four arms 76 x 9 cm radiating from the center. Mazes B and C both contained circular platforms at the end of each arm, and Mazes B and D contained only intersecting alleys at their centers. The hypothesis that the size of the central platform draws food-carrying rats to the center of the maze clearly predicts that rats should carry food only on Maze A, where the ends of the arms are narrow and the center is wide. On Mazes B and C, food is placed on the wide platforms at the end of each arm, and animals should eat at the end-of-arm locations. In the case of Maze D, the center provides no wider eating space than the arms, and animals should show no strong preference for eating in the center. On the other hand, the hypothesis that rats are drawn to the intersection of alleys predicts that rats should carry food to the center of all four mazes, since the center is always the only place where all four alleys intersect (Roberts, Phelps, and Schacter, 1989).

Insert Figure 5 about here

The percentages adjacent to each maze configuration show the percentage of opportunities that rats carried cubes of cheese weighing 2.70 grams to the center of the maze. The tendency to carry food to the center was very strong on all four mazes, with food carried 90% or more of the time on all mazes. Food carrying was reduced by 10% on Mazes B and C when compared with Mazes A and D. There was therefore a small but significant reduction in food carrying when large platforms were placed on the ends of the arms. The fact that food was carried to the center 90% or more of opportunities on all mazes strongly suggests that the dominant factor attracting animals to the center of the maze was the intersection of alleys (Roberts, Phelps, and Schacter, 1989).

The Effect of Number of Escape Routes

One interpretation of the preceding experiment is that food-carrying rats are drawn to areas where alleys intersect. One explanation of this tendency is that rats have evolved this preference through the advantage of eating at a position within a burrow system where a number of escape routes are available. A prediction from this hypothesis is that rats should be less prone to carry food to the center of a radial maze in a situation where a number of "escape routes" are also available at the end of a maze arm where food is encountered (Roberts, Phelps, and Schacter, 1989).

This prediction was examined in some experiments using several variants of the radial maze. In Figure 6, three mazes are shown that reduced the radial maze to only two alleys that radiated from a central position. All three mazes were open, elevated mazes of similar dimensions to those previously described. One arm always had two secondary arms that branched off of it, and the other arm did not. Thus, one arm had as many branches or escape routes as the center of the maze. If rats prefer to eat in the place which has the most escape routes, we should see rats eating food on the arm with two branches more frequently than on the arm with no branches (Roberts, Phelps, and Schacter, 1989).

Insert Figure 6 about here

On Maze 1, 2.70 grams cubes of cheese were placed at the end of each arm, at points A and C, and the foraging behavior of 10 rats was observed over several days. When rats found food at Point A, they always carried it to the central platform at Point B for consumption. When food was encountered at Point C, it was carried back to Point B 86% of the time and eaten at Point C 14% of the time. This experiment then provides some mild support for the prediction that rats would show a weaker tendency to carry food from an arm containing branches than from one that does not (Roberts, Phelps, and Schacter, 1989).

Stronger support for this notion was found with Maze 2, which was identical to Maze 1, except for the removal of a central platform at the intersection of the alleys. On Maze 2, rats carried food from Point D to Point E on 100% of the opportunities. Interestingly, on 90% of these occasions, the rats continued to carry the food from Point E to Point F and to eat at that point. When food was encountered at Point F, rats ate the food at that point on 86% of opportunities. Although the findings of the Experiment depicted in Figure 5 suggested that a wide circular platform in the center of a four-arm maze had only a minor effect on food-carrying behavior, a comparison of the findings from Mazes 1 and 2 with the two arms, suggests a far more potent influence exerted by the central platform. With only an intersection of alleys at the center on Maze 2, the preference for eating in the center declined substantially from that found with a wide central platform on Maze 1. The end of an alley with branches now became the favored place to consume food (Roberts, Phelps, and Schacter, 1989).

A somewhat different procedure was followed on Maze 3, since this maze was a straight alley with a wide circular platform at one end and branches at the other. Cubes of cheese were placed in the center of the alley at Point H, and a rat was then placed at Point H beside the food item. The question of interest was whether the rat would prefer to eat the food where encountered or to carry it to either the wide platform at Point G or the opposite end of the alley with branches at Point I. Rats ate the food item at Point H 28% of the time. On the remaining tests, the food was carried to Point G 7% of the time and to Point I 65% of the time. Thus, rats preferred to eat at a point where the alley bifurcated about two-thirds of the time, as opposed to eating at other places only one-third of the time (Roberts, Phelps, and Schacter, 1989).

This series of experiments generally supports the prediction that food-carrying behavior will vary significantly with the number of escape routes or alleys that branch off the end of an arm on the radial maze. To varying degrees, experiments on all three mazes showed that rats would prefer to eat food on an arm with two escape routes than on an arm with no escape routes (Roberts, Phelps, and Schacter, 1989).

In another experiment that dealt with number of escape routes, Maze 4 in Figure 7 was used, with the number of alleys branching off the end of each arm manipulated. Each arm had a central platform placed at its end. Arm A had only the single arm returning to the center attached to its end, but Arm C had a further arm extending beyond its platform. Arm B had three extra branches in addition to the alley returning to the center, and Arm D had four extra branches. Counting the total number of arms branching from each arm platform, Arms A, C, B, and D, contained 1, 2, 4, and 5 branches or escape routes, respectively (Roberts, Phelps, and Schacter, 1989).

Insert Figure 7 about here

Two rats were allowed to forage for 10 daily sessions with 2.70 gram cubes of cheese placed on each of platforms A, B, C, and D. The behavior of these animals is shown in Figure 8; proportion of food items either carried to the center or eaten on the arm is plotted against the number of escape routes available. When few escape routes were placed on the ends of the arms, rats usually carried food to the center for consumption. On Arm A, with only a single return alley, rats carried the food item to the center on 85% of the opportunities. The addition of an extra branch on Arm C had little effect, as animals carried food to the center 100% of the time from this arm. However, the tendency to carry food dropped to 80% with four escape routes on Arm B and then dropped substantially to 40% with five escape routes on Arm D (Roberts, Phelps, and Schacter, 1989).

Insert Figure 8 about here

These findings, taken in conjunction with those shown for two-arm mazes, indicate that rats' tendency to carry food to the center of a radial maze can be significantly reduced by making escape routes available on the ends of the arms of the maze. The implication of this finding is that rats normally carry large food items to the center of an unmodified maze because, in part but only in part, the center provides a position where the number of potential avenues of escape are maximized (Roberts, Phelps, and Schacter, 1989).

Effect of Conspecific on the Radial Maze

There is an assumption that rodents carry larger sized food items to safety in order to minimize risk of predation (Lima and Valone, 1986; Lima et al., 1985). The optimal foraging model implies that the presence of a predator or a conspecific ought to have an impact on foraging behavior. In the following experiment, Phelps and Roberts (1989) introduced a conspecific into the foraging environment. In one condition of the experiment, another rat was placed in a container in the center of the radial maze. If foraging on the radial maze was motivated partially by an attempt to keep food from being taken by other rats, the extent of food carrying would be reduced relative to control conditions in which a conspecific was not present.

Eleven rats were allowed to forage with 2.70 gram cubes of cheese placed on all four arms of the maze. Three different conditions were tested: a rat in a box, a box only, and the center empty. In the rat in a box condition, a transparent box that contained an adult male rat was placed in the center of the maze (Phelps and Roberts, 1989).

The probability of carrying food items from the arm to the center of the maze is shown for the three experimental conditions in Figure 9. When the center was empty or only the box was in the center, the rats carried the food to the center on 100% of the opportunities. When another rat was in the center, food carrying dropped to 70% of alley entrances (Phelps and Roberts, 1989).

Insert Figure 9 about here

The difference between the box-only condition and the rat-in-box condition is important, because it shows that carrying was not inhibited simply by the presence of an object in the center of the maze. The reduced food-carrying effect was clearly a consequence of social factors, and the findings suggest that the foraging rat was hesitant to approach an intruder while carrying food (Phelps and Roberts, 1989).

The fact that rats still returned to the center to eat 70% of the time with another rat in the center suggests that rats were under the influence of two conflicting motives. a strong tendency to carry large food items to the center, presumably shaped by evolutionary pressures to avoid predation or theft, may account for the fact that food was carried 70 % of the time. On the other hand, the need to avoid getting any closer than necessary to a conspecific while carrying food led to a 30% reduction in the normal tendency to carry a 2.70 gram item to the center on all opportunities (Phelps and Roberts, 1989).

ANALYSIS

Areas of Consensus

The research supports the notion that rats foraging on a radial maze show a number of foraging strategies that mimic those seen performed by wild rodents in more natural settings. At least three key stimulus features of the radial maze can be identified that act in concert to promote central place foraging. These are the use of large-sized food items, the intersection of alleys at a central point, and the absence of potential competitors at that point.

Gaps/Incompletions

The experiments reported thus far all conclude that a rat will bring a large food item to the center of a radial maze. Why do rats show central place foraging? There are several reasons that can be offered. One is that the center of a radial maze offers a rat more security because of its intersecting alleys (Escape Routes Model). Another is that since the center of the maze is the most frequently visited area passed on the maze, its familiarity is what attracts the rat to the center (Familiarity Model). A third, as yet untested hypothesis may be referred to as the Food Danger Model. According to this view, the most risky spot for predators or food pirates is the spot where the food has been sitting. Conversely, a safe spot would be one that had never contained any food. Perhaps what is happening in the previous studies is that the animals are moving the large cheese items to the center of the maze, not because the center of the maze is more familiar or offers more escape routes, but because it was the only place on the maze which did not have any food on it. This absence of food may have marked the center of the maze as a place of safety. Perhaps, if food was placed in the center of the radial maze, very different results might occur.

PROPOSAL

Question

My study was conducted to answer the following question: What model, Familiarity, Escape Routes, or Food Danger, best predicts where a rat will bring a piece of food to on the radial maze?

Method

Subjects

The subjects were 8 male Long Evans hooded rats (Rattus norvegicus). They were 70 days old at the start of the experiment, and 108 days old at its conclusion. The rats were housed individually and were exposed to a 16:8 light/dark schedule, with light onset at 600 hr and offset as 2200hr. Testing was performed between 1500 and 1900 hr 6 days a week. All subjects were kept at 85% of their free-holding weight.

Apparatus

The apparatus was a four-arm radial maze (See Figure 10) constructed of plywood and painted black. The four arms radiated from a circular central platform, with a 90 degree angle between adjacent arms.

The central platform was 35 cm in diameter, with each arm measuring 76 cm long x 9 cm wide. Both the center and the arms were open and contained no walls. Pieces of wooden doweling supported the arms and the central platform at a height of 60 cm above the floor.

Insert Figure 10 about here

Procedure

The items of food used on the radial maze were be pieces of Kraft American process (mild cheddar) cheese. Before the subjects were tested, a preliminary training on the maze for 11 days was conducted first to ensure that the subjects had learned to run on the maze for the cheese.

Condition 1 of this experiment was a replication of Phelps and Roberts (1989) experiment 1. In this condition, the tendency of rats to carry food items to the center of a radial maze was examined as a function of item size.

In Condition 1, food items were placed on the ends of the arms of the maze only. On any given daily session, a rat was tested with food items of the same weight on all four arms of the maze. The food items used were cubes of cheese that weighed 0.05, 0.15, 0.45, 1.35, 2.70, and 5.40 grams. Each rat was tested on all six item weights over a block of six sessions, with the order in which item weights were tested varying randomly between rats.

Condition 2 was exactly the same as Condition 1, except that food items of varying sizes (0.05 to 5.40 g) were placed in the center of the maze only, not the arms. For example, on day one of testing in this condition, a 0.05 gram cheese item was placed in the center of the maze only. The proportion of items either eaten in the center of the maze or carried to the arm of the maze was measured as a function of item weight.

At the start of each experimental session, the subjects were placed either on the center of the maze (Condition 1) or on the arms of the maze (Condition 2).

and were allowed to forage for the food. After this was done, the experimenter stood behind a door and observed the behavior of the subjects. All behaviors were recorded individually on paper that was coded for each subject.

Results

In condition 1 (Figure 11), the proportion of alley entrances on which subjects ate a food item on the arm of the maze or carried it to the center of the maze is plotted as a function of item weight.

Insert Figure 11 about here

The tendency to carry items to the center of the maze increased as the item weight increased, and the tendency to eat items on the arm of the maze decreased as the item weight increased. An Anova was completed and confirmed statistical significance F(5,35)=20.40 (see Appendix A).

In condition 2 (Figure 12), the proportion of instances where the subjects ate the food item in the center of the maze or carried it to an arm on the maze is plotted as a function of item weight.

Insert Figure 12 about here

The tendency to eat the food item in the center of the maze decreased as the item weight increased, and the tendency to carry the food item to the arm of the maze increased as the item weight increased. An Anova was completed and confirmed statistical significance F(5,35)=4.00 (see Appendix B).

Discussion

Both the findings in Condition 1 and in Condition 2 provide strong support for the food-danger model. That is, whether the food items were placed on the arms of the maze or in the center of the maze, small food items were consumed where found, but the large food items were always moved elsewhere.

Lima and his colleagues (Lima and Valone, 1986; Lima et al., 1985) suggested that central-place foraging in grey squirrels represents a trade-off between foraging efficiency and minimizing risk of predation. This position is supported by the rats' behavior on the radial maze, as suggested by the food-danger model. According to this model, the most dangerous spot on the maze is the place where the food item has been sitting; conversely, a safe spot on the radial maze would be the place which had no food placed on it. Thus, in condition 1, when food items were placed on the arms of the maze, the tendency to carry food items to the center of the maze increased as the item weight increased. In condition 2, when food items of various weights were placed in the center of the maze, the tendency to carry food items to the arms of the maze increased as the item weight increased.

Phelps and Roberts (1989) said that if the center of the radial maze is viewed by rats as a safe home base and the arms of the maze as patches, then rats, like grey squirrels, tended to carry large food items from the patch to a place of safety, and to eat small food items in the patch. The results shown in condition 2 of this current study do not provide support for the center of the maze being viewed as a safe home base, since when food was placed in the center of the maze, the rats moved the large food items to the arms of the maze.

I think that the radial maze has ecological validity for studying central-place foraging in rats. But, there are some loose ends that still need to be examined. If the rat does not view the center of the maze as the safest spot on the maze, then is there a spot on the maze in which the rat views as safe? Or is it a case that there is no safe spot on the maze - that the rat just moves a big piece of food elsewhere?

References

Barnett, S.A. (1975). The Rat. Chicago: Chicago University Press.

Bindra, D. (1948b). What makes rats hoard. Journal of Comparative and Physiological Psychology, 41, 397-402.

Explains that a rat will transport a particular material to its cage if (1) that material is valuable to the rat, and (2) there is a certain optimum difference in the security offered by the cage and the security offered by the place where the material is to be found.

Covich, A.P. (1987). Optimal use of space by neighboring central place foragers: When and where to store surplus resources. In L. Green and H. Kagel (Eds.), Advances in Behavioral Economics (pp. 249-294). Norwood, N.J.: Ablex.

Flannelly, K.J., and Lore, R. (1977). Observations of the subterranean activity of domesticated and wild rats (*Rattus norvegicus*): A Descriptive Study. Psychological Record, 27, 315-329.

Flannelly, K.J., Kemble, E.D., and Hori, K. (1986). Structure, content, and distribution of roof rat (_Rattus_ _rattus_) burrows in a rain forest. _Journal of Comparative Psychology_, _100_, 208-214.

Roof rat burrows were excavated in a rain forest in Hawaii. Few burrows contained nest material or food, but evidence of feeding stations were found.

Ilersich, T.J., Mazmanian, D.S., and Roberts, W.A. (1988). Foraging for covered and uncovered food on a radial maze. _Animal Learning and Behavior_, _16_, 388-394.

Rats were trained to forage for food on a four-arm radial maze. With open feeders, rats visited feeders in order; with covered feeders, rats visited feeders containing the most pellets first.

Lima, S.L. (1985). Maximizing feeding efficiency and minimizing time exposed to predators: A trade-off in the black-capped chickadee. _Oecologia_, _66_, 60-67.

It was found that free-ranging chickadees foraging at an artificial patch at various distances from cover can

distinguish between maximizing foraging efficiency and minimizing exposure time.

Lima, S.L., and Valone, T.J. (1986). Influence of predation risk on diet selection: A simple example in the grey squirrel. Animal Behavior, 34, 536-544.

Grey squirrels (Sciurus carolinensis) may reject more energetically profitable, but small food items in favor of locating larger, less energetically profitable items that can be carried to protective cover for consumption without greatly sacrificing foraging efficiency.

Lima, S.L., Valone, T.J., and Caraco, T. (1985). Foraging efficiency predation risk trade-off in the grey squirrel. Animal Behavior, 33, 155-165.

The hypothesis that grey squirrels are trading off energy intake rate against predation risk was tested by presenting free-roaming grey squirrels with patches containing a fixed number of identical food items. The hypothesis was supported.

Lore, R. and Flannelly, K. (1978). Habitat selection and burrow construction by wild _Rattus norvegicus_ in a landfill. _Journal of Comparative and Physiological Psychology_, _92_, 888-896.

Rat burrows were examined. It was found that rats selected burrow sites that minimized the travel distance to the major food source and a permanent water supply.

Mellgren, R.L., Misasi, L., and Brown, S.W. (1984). Optimal foraging theory: Prey density and travel requirements in _Rattus norvegicus_. _Journal of Comparative Psychology_, _98_, 142-153.

Two rats were allowed to forage for food by climbing nail ladders to a box containing "prey" mixed with sand. The amount of food was varied, as was the distance each patch was placed above the ground under conditions of constant patch height and differing locations of patch densities. Both subjects showed optimal usage of the patches.

Olton, D.S., and Samuelson, R.J. (1976). Remembrance of places passed: Spatial memory in rats. Journal of Experimental Psychology: Animal Behavior Processes, 2, 97-116.

Rats were tested on a 8-arm radial maze. Data suggest that there was no tendency to generalize among spatially adjacent arms.

Pisano, R.G., and Storer, T.I. (1948). Burrows and Feeding of the Norway Rat. Journal of Mammalogy, 29, 374-383.

This article describes in full detail, the burrow construction and feeding habits of the Norway rat.

Phelps, M.T., and Roberts, W.A. (1989). Central place foraging by Rattus norvegicus on a radial maze. Journal of Comparative Psychology, 103, 326-338.

Central place foraging in rats was studied by placing food items that varied in size and weight at the ends of a four-arm radial maze. Results indicate that rats increasingly tended to carry food to the center of the maze as the size of those items increased.

Pyke, G.H., Pulliam, H.R., and Charnov, E.L. (1977). Optimal foraging: A selective review of theory

and tests. The Quarterly Review of Biology, 52, 137-154.

Optimal foraging theory can be divided into four categories: (1) optimal diet; (2) optimal patch choice; (3) optimal allocation of time to different patches; and (4) optimal patterns and speed of movements.

Roberts, W.A. (1984). Some issues in animal spatial memory. In H.L. Roitblat, T.G. Bever, and H.S Terrace (Eds.), Animal Cognition (pp 425-443). Hillsdale, N.J.: Erlbaum.

Roberts, W.A. (1989, April). Foraging on a Radial Maze: Learning, Memory, and Decision Rules. Paper presented at the University of Iowa Conference on Learning and Memory: Behavioral and Biological Substrates.

A series of experiments shows that rats foraging on a radial maze are sensitive to several variables that are relevant to foraging in a natural setting. These variables include differences in density of food among patches, location of food within a patch, and properties of food items, such as number and size.

Roberts, W.A., Phelps, M.T., and Schacter, G.B. (1989, June). *Stimulus Control of Central Place Foraging on the Radial Maze*. Paper presented at the Dalhousie Conference on Cognitive Aspects of Stimulus Control.

It was shown that three key stimulus features of the radial maze act in concert to promote central place foraging. These include the presence of open alleys, the use of large sized food items, and the intersection of alleys at a central place.

Takahashi, L.K., and Lore, R.K. (1980). Foraging and food hoarding of wild *Rattus norvegicus* in an urban environment. *Behavioral and Neural Biology*, *29*, 527-531.

The foraging activities of a free-living population of wild *Rattus norvegicus* was examined. Subsequent excavation of the burrow systems of these animals revealed no evidence that food had either been consumed or stored in the burrows.

Vander Wall, S.B. (1990). Food Hoarding in Animals. Chicago: Chicago University Press, 1.

This book is an indepth look at food hoarding in various animals.

Viek, P. and Miller, G.A. (1944). An analysis of the rat's response to unfamiliar aspects of the hoarding situation. Journal of Comparative Psychology, 37, 221-231.

Strangeness in any of the three aspects studied, the cage, the alley, or the pellets, will affect the hoarding behavior in rats. Of these three aspects, the rat's familiarity with the cage seems most important, and familiarity with the pellets of least importance.

Whishaw, I.Q., and Tomie, J. (1989). Food pellet size modifies the hoarding behavior of foraging rats. Psychobiology, 17, 93-101.

Rats were allowed to forage for different sized food pellets from a cage attached to a straight alley or form a cage placed in the center of an 8-arm radial maze. In both tasks, food pellet size influenced motor responses.

Appendix A

Summary Table:

The Following is a summary table for the results in Condition 1.

Source	df	SS	MS	F
Between Subjects	7	17.5		
Items	5	97.88	19.58	20.40*
Error	35	33.62	0.96	
Total	47	149.00		

*$p < 0.05$

Appendix B

Summary Table:

The following is a summary table for the results in Condition 2.

Source	df	SS	MS	F
Between Subjects	7	1.14		
Items	5	2.19	0.44	4.00*
Error	35	3.98	0.11	
Total	47	7.31		

*$p < 0.05$

Figure Captions

Figure 1. Curves showing the mean pellets consumed at the first, second, third, and fourth feeder visited by rats in the covers and open feeders groups. Each point represents mean pellets consumed over all four patches and over days 2-10 of testing.

Note. Reprinted by permission

Figure 2. Effect of food size on behavior in a straight alley. "Eat" = food eaten while standing; "sit" = food eaten after rat adopted a sitting posture; and "hoard" = food transported to the home cage. Small pellets were eaten while rats were standing, medium-sized pellets were eaten while rats were sitting, and large pellets were hoarded.

Figure 3. Effect of food-pellet size on behavior in an 8-arm radial maze. Each arm was baited with one pellet size, and the amount of food in each arm was equivalent. Note that as pellet size increased, behavior changed from swallowing ("eat") to sitting up and eating ("sit") to hoarding ("hoard").

Figure 4. Proportion of items eaten on an arm of the maze or carried to the center of the maze, plotted as a function of item weight.

Note. Reprinted by permission.

Figure 5. This diagram shows four open mazes on which either wide circular platforms or narrow alleys were placed in the center and at the ends of the arms. The percentages beside each maze indicate the percentage of opportunities that a food item was carried to the center of the maze.

Note. Reprinted by permission.

Figure 6. Diagrams of three two-arm mazes.

Note. Reprinted by permission.

Figure 7. Diagram of one four-arm maze. The arms of the maze contain different numbers of branches or escape routes.

Note. Reprinted by permission.

Figure 8. Proportion of 2.70 gram food items that were carried to the center of Maze 4 or were eaten on the arm, plotted as a function of arms, containing 1, 2, 4, or 5 escape routes.

Note. Reprinted by permission.

Figure 9. Proportion of 2.70 gram food items carried to the center of the maze when the center was empty, contained an empty box, or contained a rat in the box.

Note. Reprinted by permission.

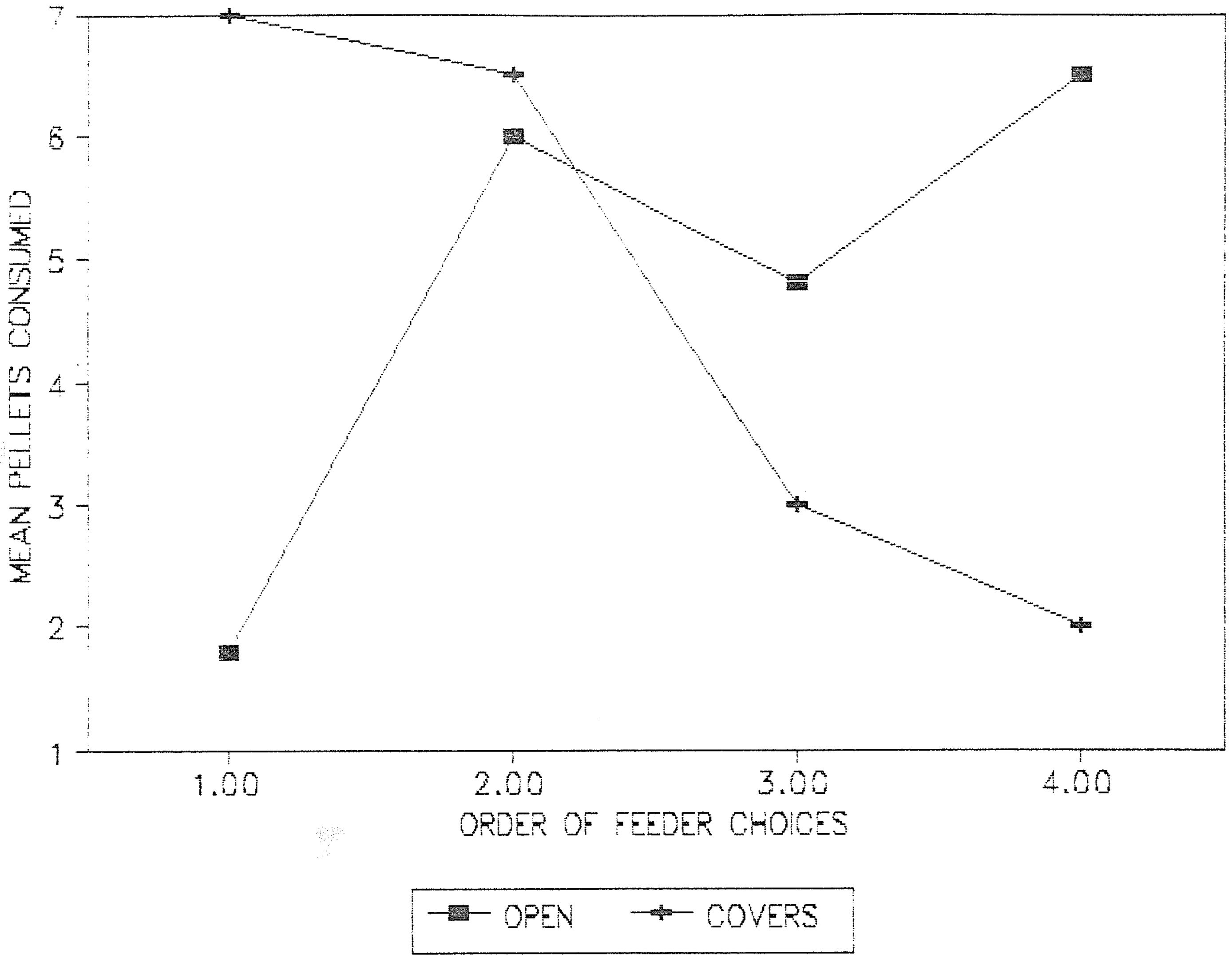
Figure 10. Standard Four-arm radial maze.

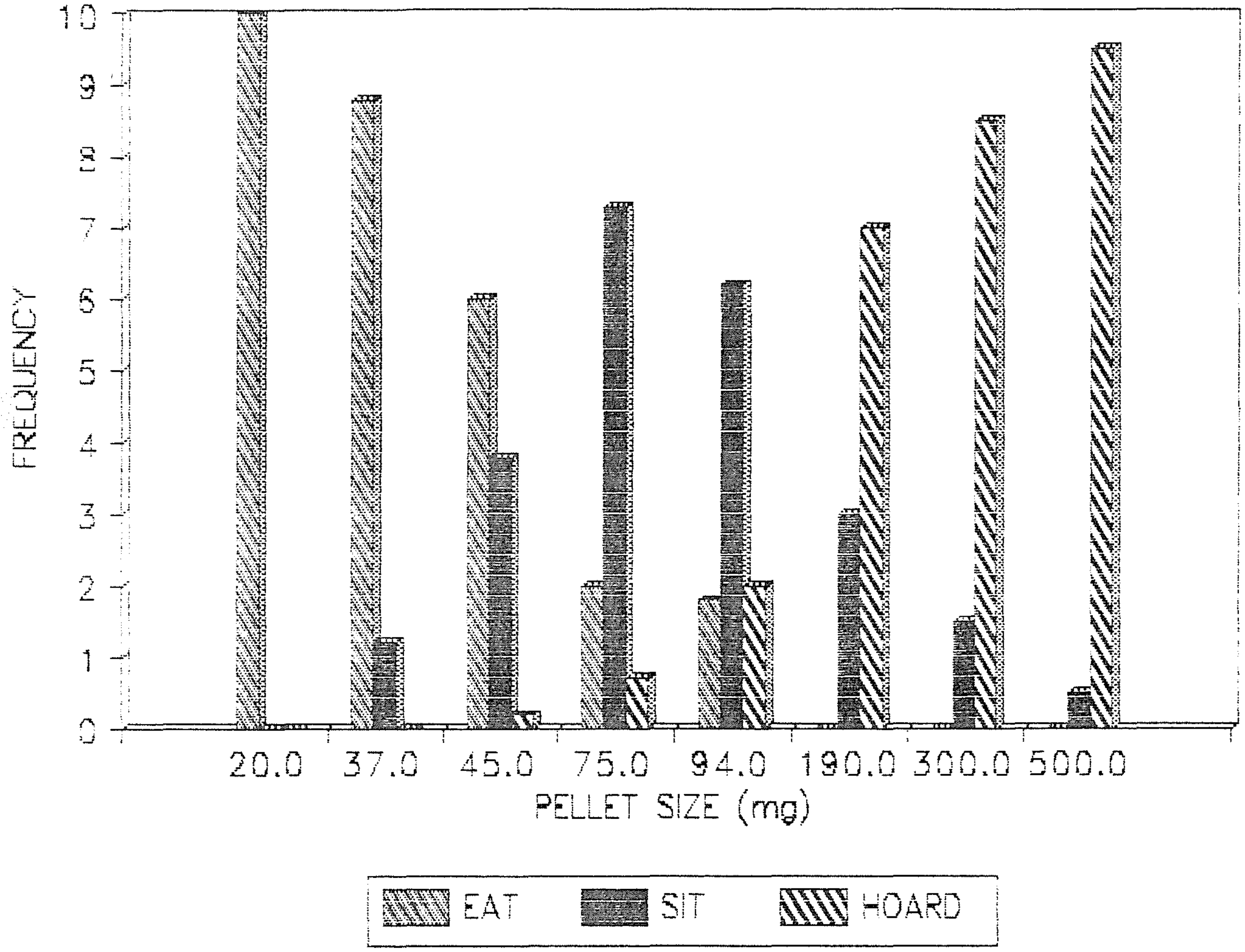
Note. Reprinted by permission.

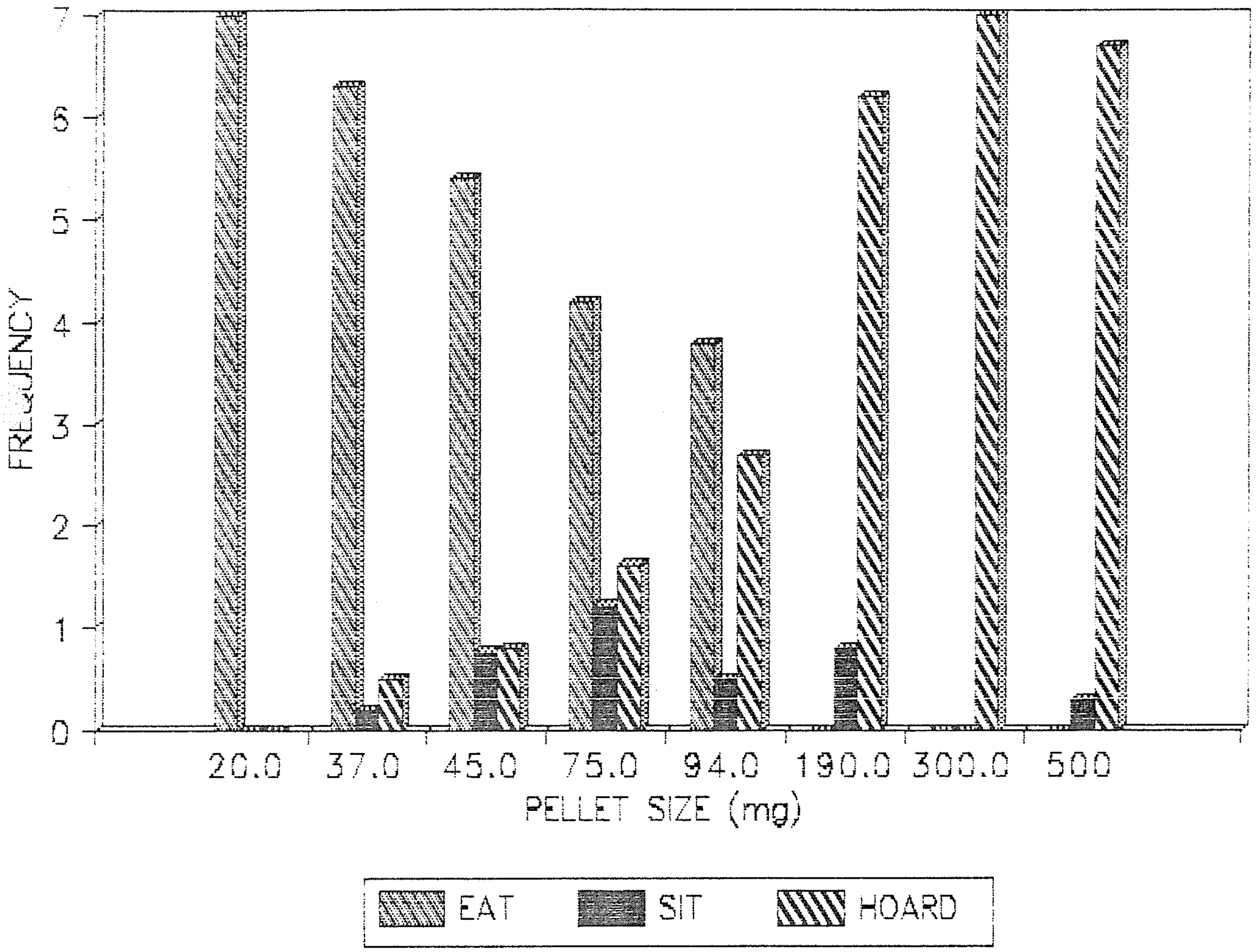
Figure 11. Proportion of items eaten on an arm of the maze or carried to the center of the maze, plotted as a function of item weight.

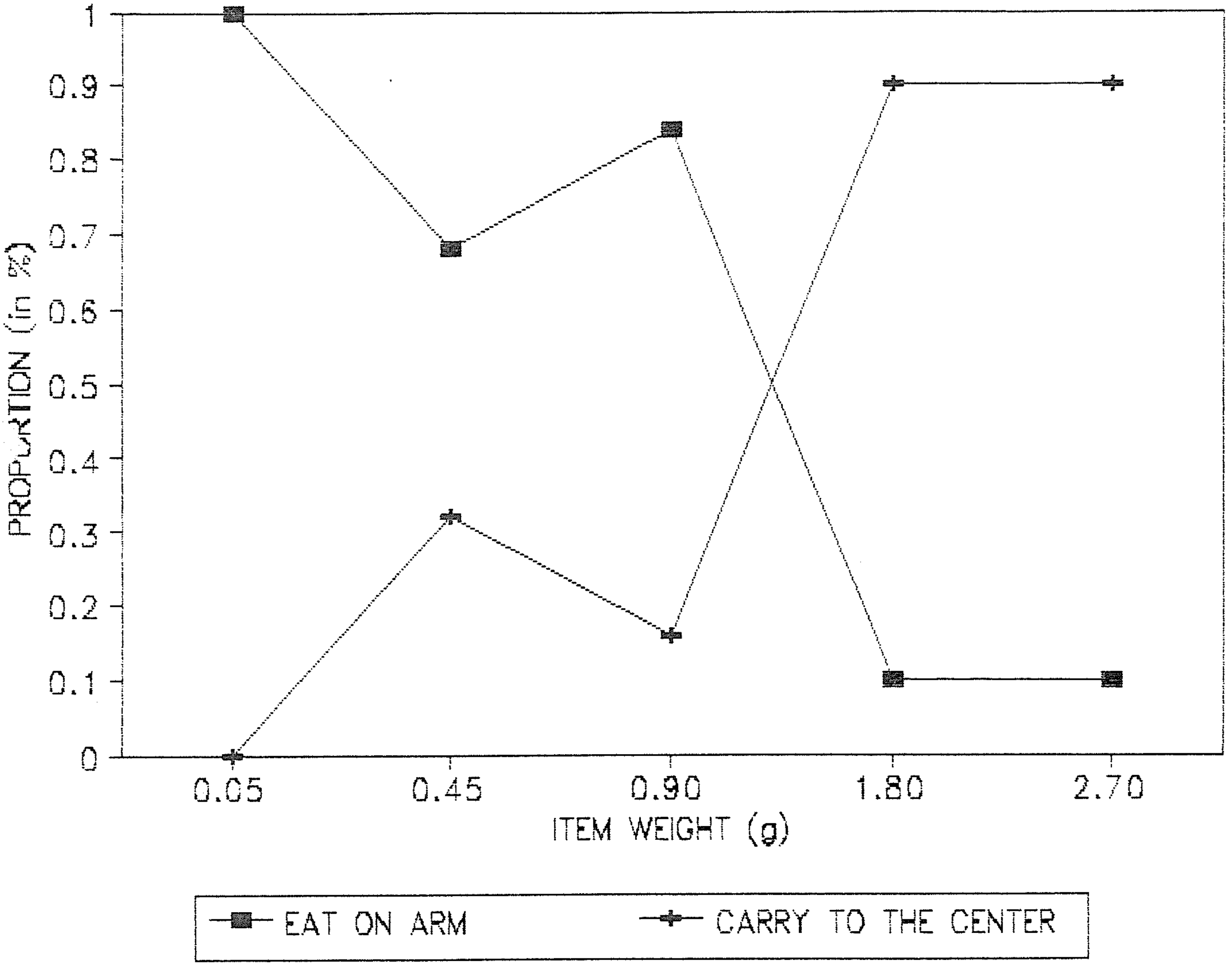
Note. Reprinted by permission.

Figure 12. Proportion of items eaten in the center of the maze or carried to the arms of the maze, plotted as a function of item weight.


MEAN PELLETS CONSUMED
1
2
3
4
5
6
7
1.00
2.00
3.00
4.00
ORDER OF FEEDER CHOICES
OPEN
COVERS

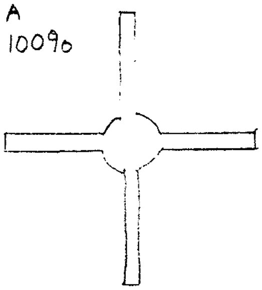

10
9
8
7
6
5
4
3
2
1
0
FREQUENCY
20.0
37.0
45.0
75.0
94.0
190.0
300.0
500.0
PELLET SIZE (mg)
EAT
SIT
HOARD


FREQUENCY
0
1
2
3
4
5
6
7
20.0
37.0
45.0
75.0
94.0
190.0
300.0
500
PELLET SIZE (mg)
EAT
SIT
HOARD

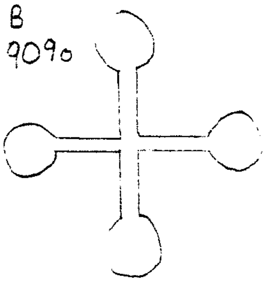


1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
PROPORTION (in %)
0.05
0.45
0.90
1.80
2.70
ITEM WEIGHT (g)
EAT ON ARM
CARRY TO THE CENTER

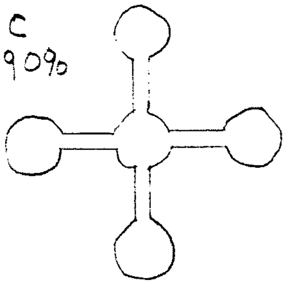
A
100%



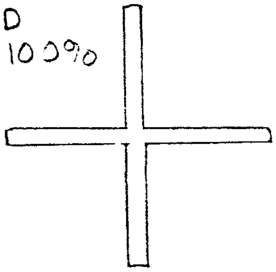
B
90%



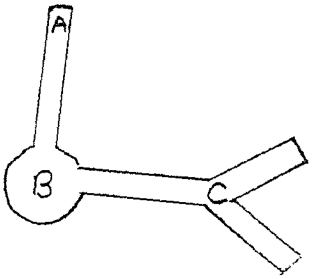
C
90%



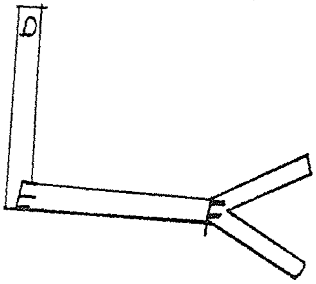
D
100%



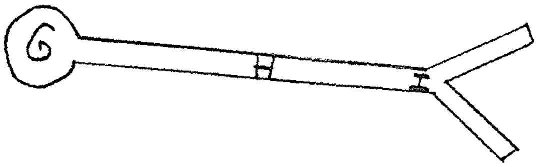
maze 1



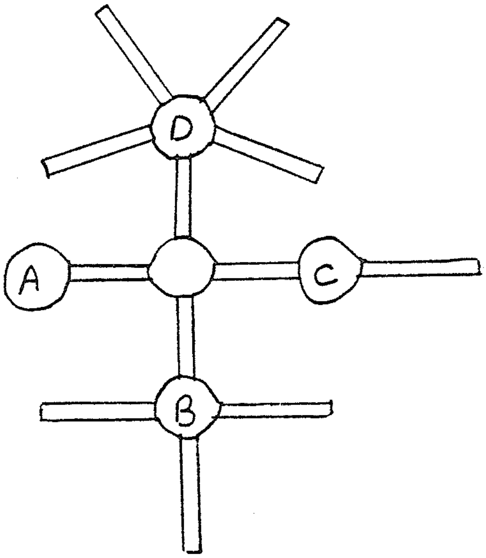
maze 2

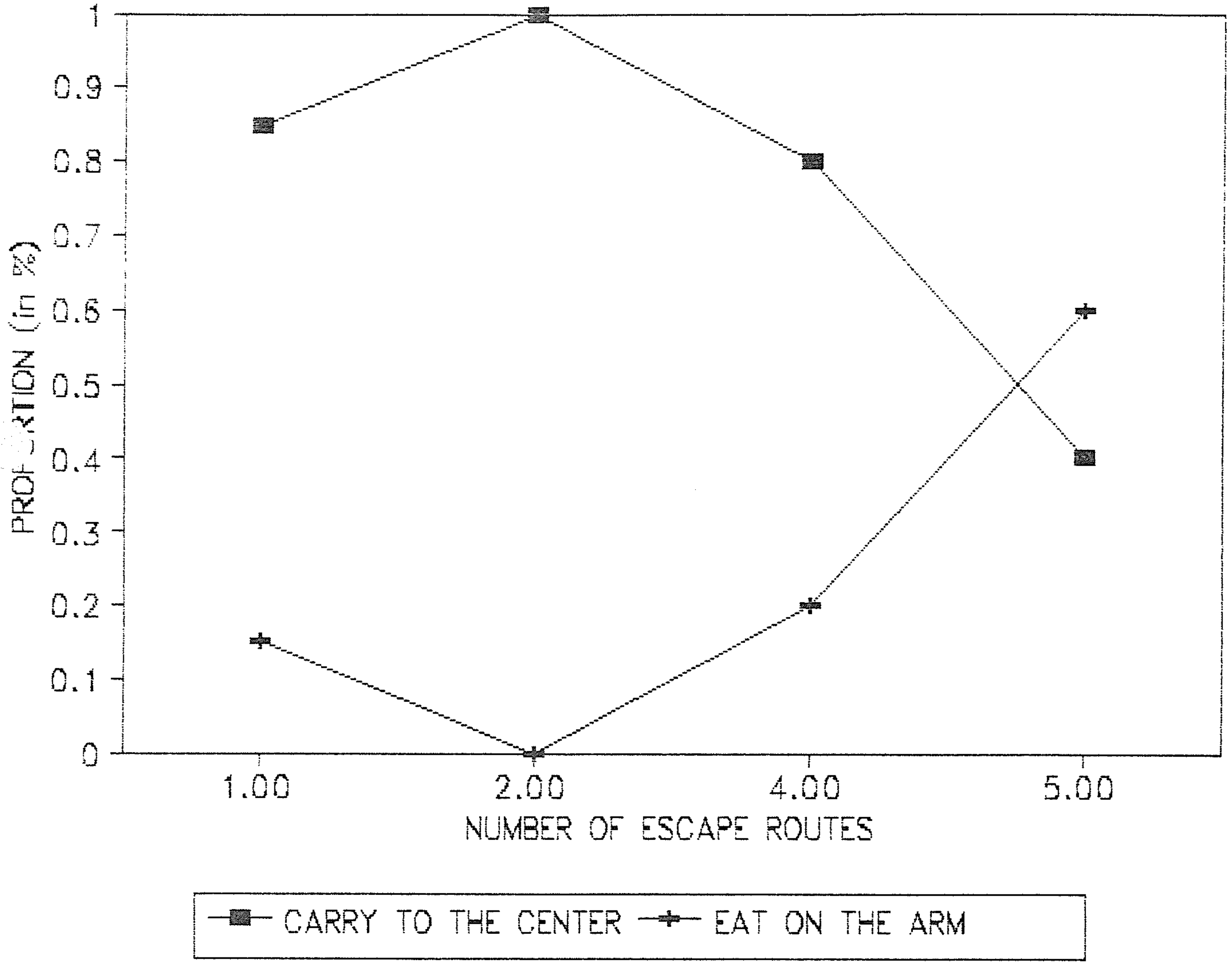


maze 3

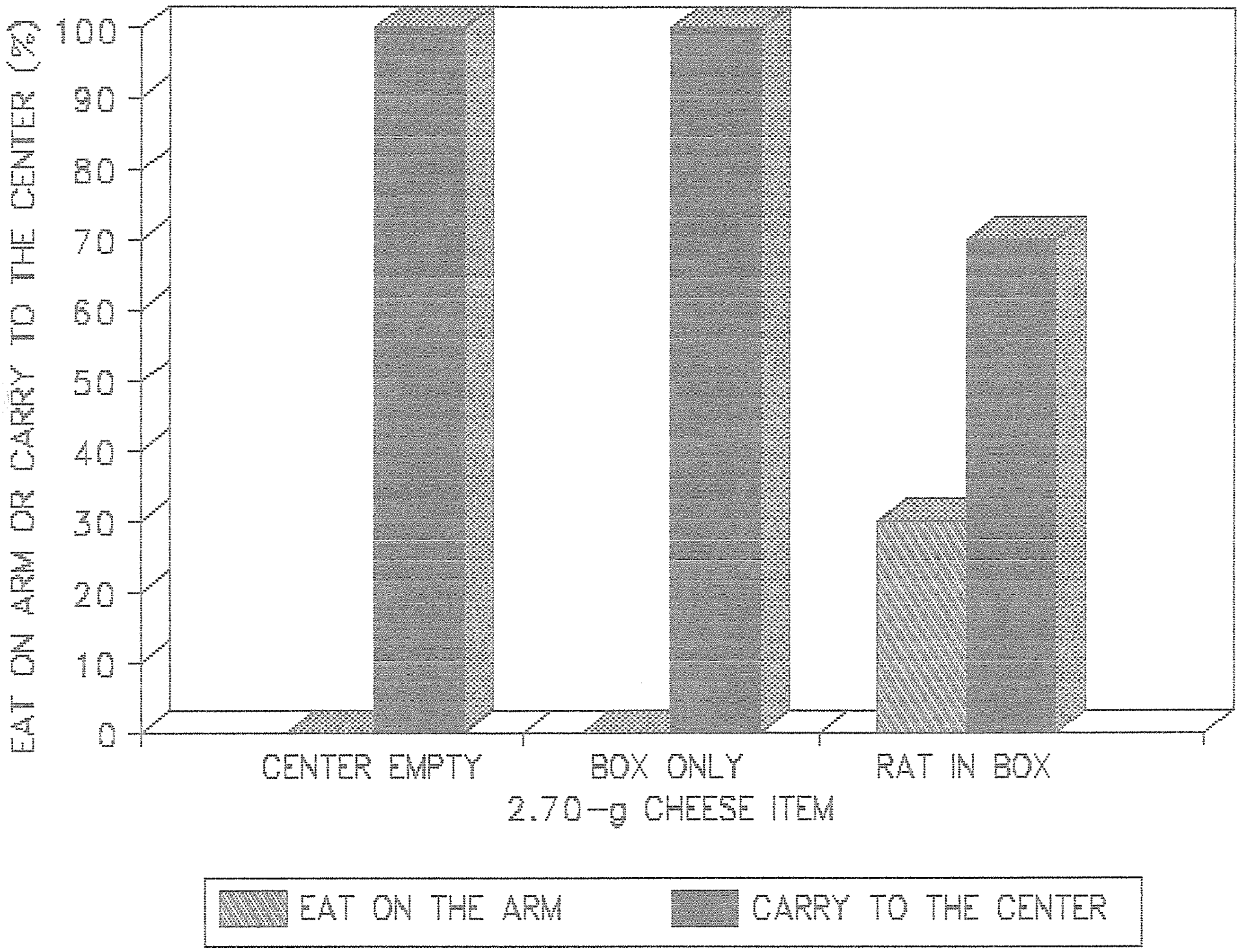


MAZE 4

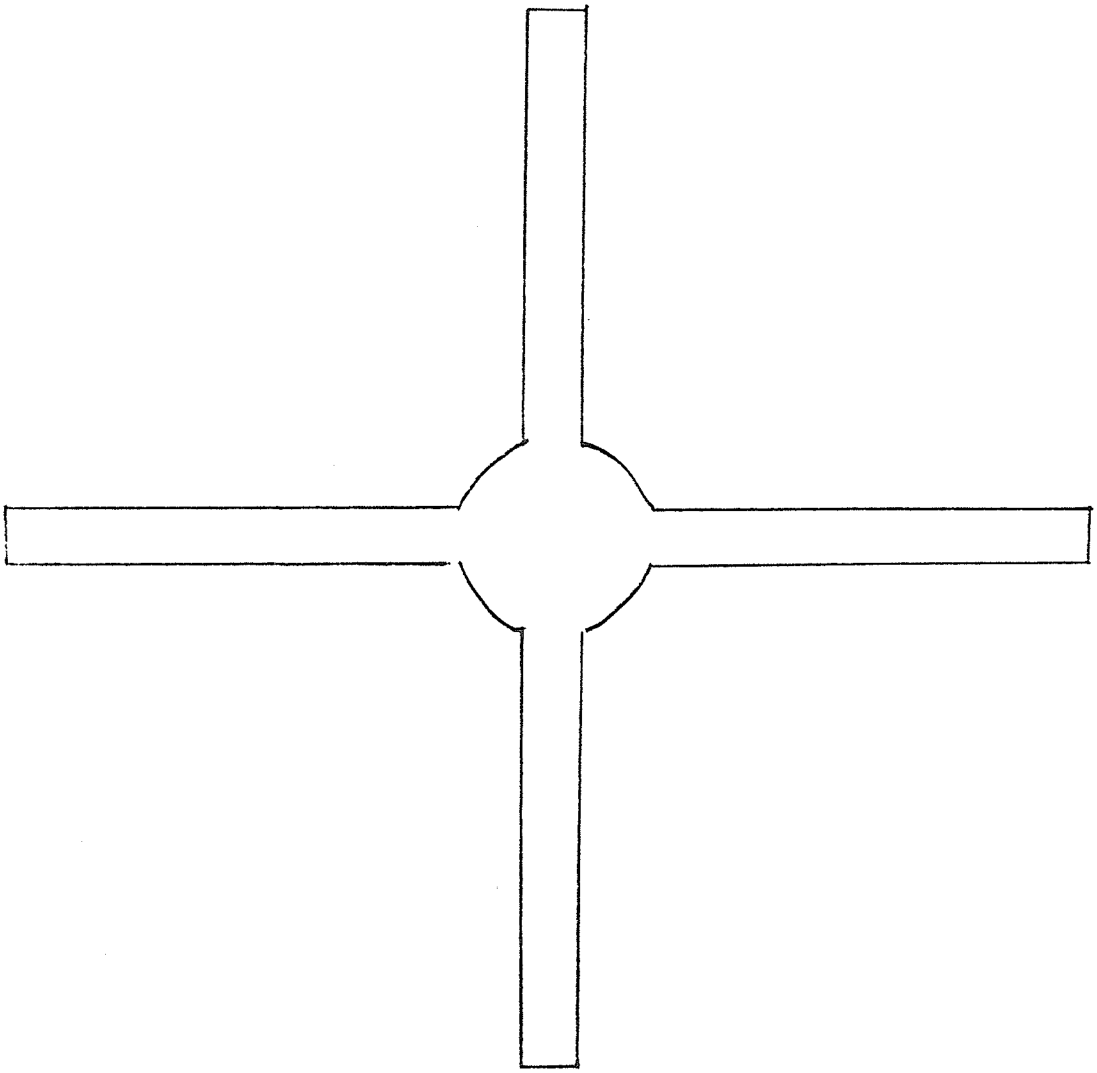


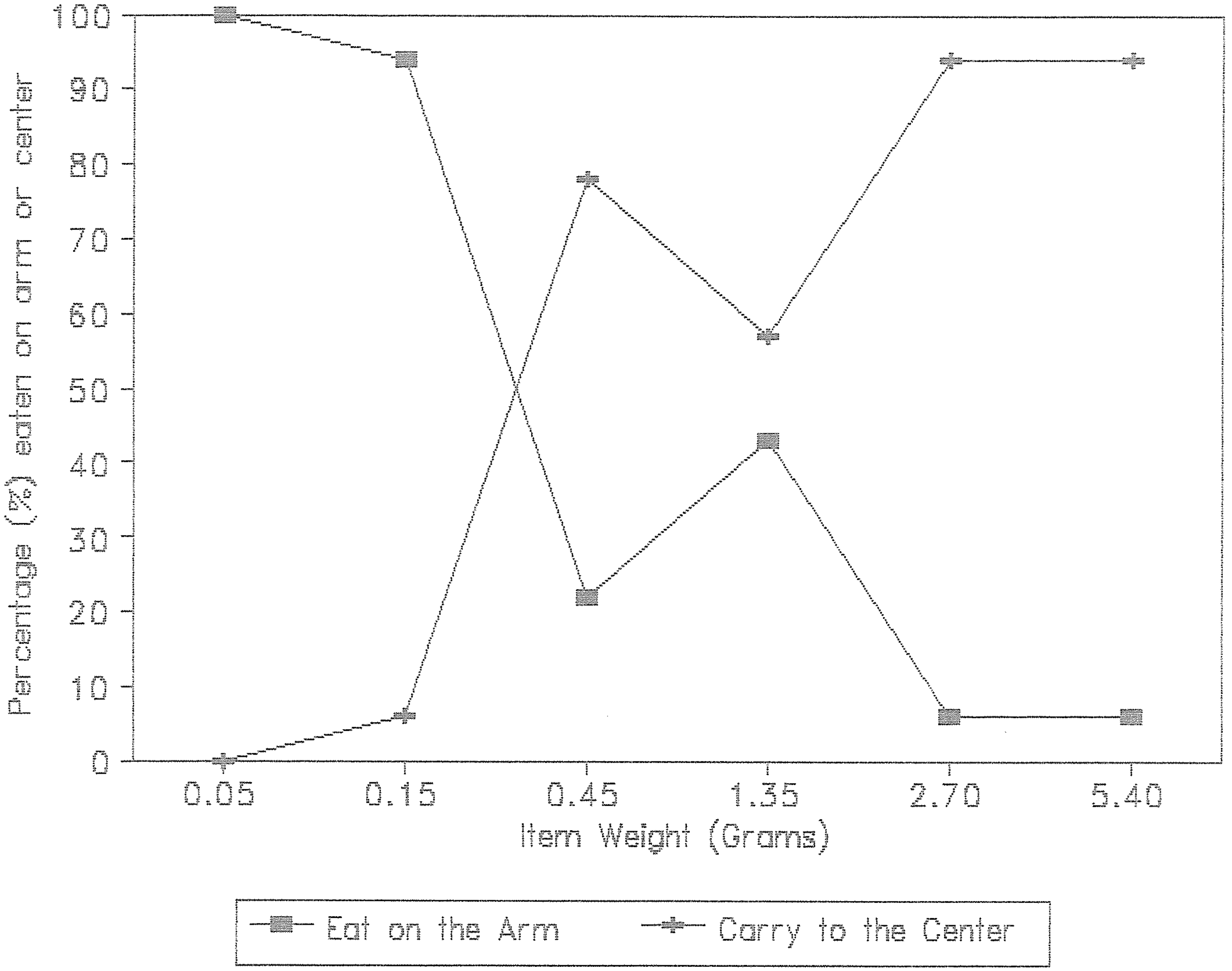


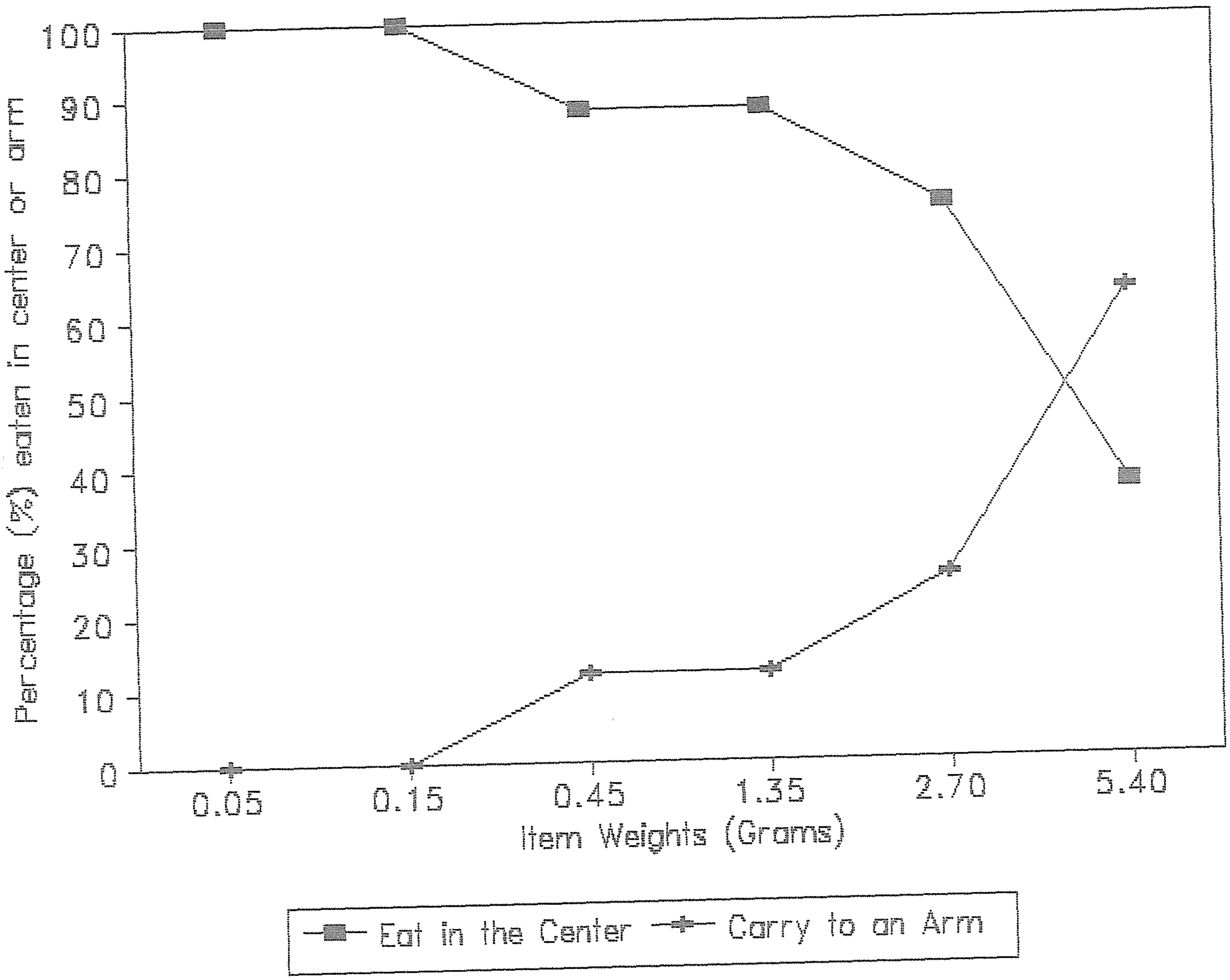
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
PROPORTION (in %)
1.00
2.00
4.00
5.00
NUMBER OF ESCAPE ROUTES
CARRY TO THE CENTER
EAT ON THE ARM



EAT ON ARM OR CARRY TO THE CENTER (%)
0
10
20
30
40
50
60
70
80
90
100
CENTER EMPTY
BOX ONLY
RAT IN BOX
2.70-g CHEESE ITEM
EAT ON THE ARM
CARRY TO THE CENTER




100
90
80
70
60
50
40
30
20
10
0
Percentage (%) eaten on arm or center
0.05
0.15
0.45
1.35
2.70
5.40
Item Weight (Grams)
Eat on the Arm
Carry to the Center



100
90
80
70
60
50
40
30
20
10
0
Percentage (%) eaten in center or arm
0.05
0.15
0.45
1.35
2.70
5.40
Item Weights (Grams)
Eat in the Center
Carry to an Arm

PSYC 4105; Self-Evaluation Form

Please Complete Form and Submit it with Final Copy of Thesis:

Your Name: Shelley May

As you know, a single grade must ultimately be assigned covering all the work done this year in this course. I am asking for your opinion to assist in this process.

Basis for Evaluation:

As described in the Course Outline, the principal activities/ assignments for this course were:

a) discussion of topics and designs
b) preparation of research proposal
c) execution of data-collection
d) statistical analysis of results
e) preparation of final written version of Thesis
f) oral presentation at AUC Thesis Conference

The grade is to be a "balanced weighting of the above factors, with greatest emphasis on the final product."

Scale:

Grades will be assigned on a numerical scale corresponding to the following categories:

80 - 100: Exceptional Performance; normally this involves not only mastery of required work, but original and independent application of knowledge.

70 - 79: Good Performance; thorough understanding, competent work.

60-69: Satisfactory: note that for a Thesis, grades in this range indicate performance which meets ordinary undergraduate standards, but is not at an "Honors" level.

50-59: Minimally Competent Performance: not satisfactory for the course, but still deserving of academic credit.

Your Evaluation:

Based on the assignments and scale above, please indicate the numerical grade corresponding to:

1) The **HIGHEST** grade you realistically think you might get. 90

2) The **LOWEST** grade you realistically think you might get. 80

3) The grade you would assign to your work: 85